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Desert endophytic fungi improve reproductive, morphological, biochemical, yield and fruit quality characteristics of tomato under drought stress

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Abstract

Purpose – Crops are increasingly affected by drought; hence, the current study explored the potential role of three desert endophytic fungi, *Aspergillus fumigatus*, *Aspergillus terreus* and *Talaromyces variabilis*, in conferring drought tolerance in tomato plants.

Design/methodology/approach – Preserved endophytic fungi from a *Rhazya stricta* desert plant were adopted to obtain the required fungal treatment; tomatoes received fungal treatments directly in plastic trays and subsequently in pots. Drought was applied using 15% of PEG-6000 at two stages: flowering and fruiting. The following parameters were measured: pollen sterility, growth characteristics, morphological analysis and biochemical analysis, including proline, gibberellic acid (GA3) and chlorophyll measurements; thus, the data were analyzed statistically using SPSS software.

Findings – All applied endophytes significantly promoted pollen viability and tomato yield under stressed and nonstressed conditions. Interestingly, these endophytes significantly enhanced the number of trichomes under drought stress and promoted tomato fruit quality. The colonized tomato plants accumulated a high proline level under drought stress but lower than un-inoculated stressed plants. Also, a significant rise in growth characteristics was observed by *A. fumigatus* and *A. terreus* under normal conditions. Moreover, both raised GA3 levels under drought-stressed and nonstressed conditions. Also these two endophytes enhanced chlorophyll and carotenoid contents under drought stress. Fruit characteristics were enhanced by nonstressed *T. variabilis* and stressed *A. fumigatus*.

Originality/value – The present endophytic fungi provide impressive benefits to their host in normal and drought-stressed conditions. Consequently, they represent valuable sources as sustainable and environmentally friendly alternatives to mitigate drought stress.

Keywords Abiotic stress, *Aspergillus fumigatus*, *Aspergillus terreus*, Endophytes, *Talaromyces variabilis*, Trichomes

Paper type Research paper

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1. Introduction

Climate change is accelerating, negatively affecting agriculture, reducing yield productivity and putting food security and people's lives at risk. Hence, crops and agricultural adaptation are strongly required (Anderson, Bayer, & Edwards, 2020; Parry, 2019; Westengen & Brysting, 2014). Drought is a disastrous phenomenon that increased in the last century and is most likely to rise due to climate change (Jehanzaib & Kim, 2020). Several reports proved the considerable reduction in crop yield in many countries under drought conditions (Chen, Liang, Liu, Jiang, & Xie, 2018; Ray, Fares, & Risch, 2018). Other essential features of plants were also affected by drought stress, including growth parameters, physiological and biochemical attributes, morphological characteristics, reproductive development and seed germination (Halo, Al-Yahyai, & Al-Sadi, 2020; Muscolo, Sidari, Anastasi, Santonoceto, & Maggio, 2014; Yaseen *et al.*, 2020).

The previous destructive effects of drought on plants and the agriculture sector encourage farmers, scientists and researchers to mitigate this mounting problem. Improving drought tolerance is a constructive attempt to overcome drought impact; this include traditional and molecular breeding (Ali, Rai, Jan, & Raina, 2022; Cuc *et al.*, 2021), exogenous substances application (Nazar *et al.*, 2020), metabolic engineering (Ilyas *et al.*, 2020) and microbial inoculation (Azeem, Haider, Javed, Saleem, & Alatawi, 2022; Yasmin *et al.*, 2022). Recently, there has been growing interest to enhance drought tolerance in crops using endophytic inoculation (Morsy, Cleckler, & Armuelles-Millican, 2020; Sadeghi, Samsampour, Seyahooei, Bagheri, & Soltani, 2020).

Endophytic fungi provide multiple benefits to their hosts in normal conditions (Khan *et al.*, 2015). Also, they enhance the ability of their hosts to survive under extreme conditions such as biotic stress (Halo, Al-Yahyai, & Al-Sadi, 2018; Halo, Al-Yahyai, Maharachchikumbura, & Al-Sadi, 2019) and abiotic stress, including drought, salinity and heat (Bilal *et al.*, 2020; Hubbard, Germida, & Vujanovic, 2014; Khan *et al.*, 2011). Regarding their role in water use efficiency, it was found the inoculation with root-endophytes maintained higher water use efficiency and enhanced net photosynthesis in drought conditions; moreover, these are correlated with greater fresh and dry biomass production and better root system development (Molina-Montenegro *et al.*, 2016).

The previous reports attempted to clarify this remarkable role of endophytes, but the mechanisms were not fully clear, principally related to the activation of the host response system (Khare, Mishra, & Arora, 2018); however, some mechanisms were evident such as the production of phytohormones and other efficacious secondary metabolites, induction expression of the stress-responsive genes and activation of silent gene clusters resulting in production metabolites (Dinesh, Srinivasan, TE, Anandaraj, & Srambikkal, 2017; Nataraja, Dhanyalakshmi, Govind, & Oelmüller, 2022).

Several plant features have got attention in studying the effect of endophytic treatments under drought stress, such as growth, biochemical, physiological and molecular characteristics; however, some features received little attention despite their great importance, such as reproductive and morphological features; hence, pollen viability and trichomes and stomata density were investigated in our study.

Tomato (*Lycopersicon esculentum* Mill.) is a herbaceous and dicotyledonous plant, highly branched and spreading between 60–180cm with phyllotaxy leaf arrangement; a terminal bud provides the actual growing at the apex of the stem; the flowers are pendant and clustered. Fruits are valuable sources of folate, vitamin C and minerals; also, high carotenoid content in tomato fruits increases their antioxidant activity (Beecher, 1998). However, drought caused harmful impacts on tomato growth and yield (Cui, Shao, Lu, Keabetswe, & Hoogenboom, 2020; Zhou *et al.*, 2017).

A. fumigatus, *A. terreus* and *T. variabilis* endophytes were reported for their efficient role as plant enhancing survival and growth under abiotic stress conditions. Also, they serve as effective antagonistic agents against plant pathogens (Halo *et al.*, 2018, 2019; Khan *et al.*, 2011; Khushdil *et al.*, 2019); furthermore, both *A. terreus* and *A. fumigatus* endophytes are valuable sources of bioactive metabolisms, including antioxidants, antitumors, biopharmaceuticals and phytohormones; consequently, they are utilized widely for medical, agricultural and industrial purposes (El-Sayed *et al.*, 2021; Hussein *et al.*, 2022; Xiao-Feng *et al.*, 2021); however, the bio-role of *T. variabilis* endophyte was not well investigated.

To our knowledge, few studies have investigated the role of endophytic fungi in improving crop yield under drought conditions; also, the current endophytes have not yet been investigated in promoting drought tolerance in tomatoes. Furthermore, applying excessive-habitat-adapted symbiotic microbes is a well-known effective mechanism to mitigate the devastating impacts of abiotic stresses (Moghaddam, Safaie, Soltani, & Hagh-Doust, 2021). Accordingly, our selected desert endophytic fungi are most likely adapted to drought stress conditions. Thus, the present study investigated whether these endophytes (independent variables) can enhance plant features (dependent variables: growth, yield, morphological and biochemical characteristics) to provide drought tolerance to their hosts (the primary purpose).

2. Materials and methods

2.1 Experimental design and treatment applications

The treatments were the fungal treatments with and without drought application: nonstressed *A. fumigatus* (10P), stressed *A. fumigatus* (D10P), nonstressed *A. terreus* (65P), stressed *A. terreus* (D65P), nonstressed *T. variabilis* (48P), stressed *T. variabilis* (D48P), the control (W) and the drought stress (D) treatments. The endophytes were obtained from preserved collections of the Plant Sciences Department at Agricultural and Marin Sciences College, Sultan Qaboos University (SQU). All of them were isolated from *Rhazya stricta* desert plant in an arid location in Oman.

The steps provided in our previous paper, Halo *et al.* (2020), were followed to carry out the experiment, that confirmed the advantageous role of an endophytic *Talaromyces omanensis* in mitigating drought stress in tomatoes; accordingly, the seeds were surface sterilized, fungi were grown in potato dextrose broth for 10 days to get a fungal suspension and the compost soil was autoclaved twice, which has the following composition: sphagnum peat (0.3 m dark and 0.6 m light (layer thickness)), nutrient added in peat per m^3 include 1.1 Kg base fertilizer NPK 14-16-18. 4.5 kg LIME/Dolodust, 0.4 Liter wetting agent with a pH value of 4.5–5.5, organic matter 91.4% (w/w), C/N ratio: 36.6, sodium chloride: 850 mg/kg, moisture content 38.5% (w/w) (BULRUSH, Bellaghy, UK), the seeds were sown in plastic trays at the first step and some received a fungal suspension; the tiny seedlings were transferred to their appropriate pots (30-cm diameter) under glasshouse conditions at SQU (approx. 75% RH, 28°C, latitude: 23°36'N and altitude: 51 m above sea level), these include pots with pure compost soil for control and nontreated stressed groups, pots with compost soil mixed with fungal suspension for fungal treatment groups, each pot was mixed with one liter of fungal suspension. Drought was applied using 15% of PEG-6000 at two stages: flowering and fruiting for nine days. During both stages, 0.5 liters of PEG was applied daily for each plant (Halo *et al.*, 2020). Three pots were set for each treatment, with three seedlings in each. All parameters were measured after the second drought application (fruiting stage) except pollen sterility which was detected after the first one.

2.2 Pollen sterility and growth characteristics

The acetocarmine staining test was used to calculate pollen sterility (Fernandez-Munoz, Gonzalez-Fernandez, & Cuartero, 1994). Pollen was taken from flowers on the lowest three inflorescences (Abdul-Baki, 1992). The experiment was repeated three times.

The features of the shoot and root (length and fresh and dry weight), in addition to the leaf area, were measured. For dry weight, samples were dried in an oven until they reached a constant weight. The fourth branch from the top was selected to measure the leaf area. All nine replicates were used for shoot features; however, seven were selected randomly for root features.

2.3 Fruit characteristics

The total number of fruits and number of ripe and mature fruits were counted for all replicates; however, fruit weight and size were measured for 10 random samples.

The following biochemical characteristics of tomato fruit juice were detected: pH, titratable acidity and total soluble solids (°Brix). Titration to pH 8.3 was obtained using 0.1 NaOH, the values of titratable acidity were expressed as anhydrous citric acid, and the applied formula was: % acid = ([mls NaOH used] × [0.1 N NaOH] × [milliequivalent factor] × [100])/grams of sample (Garner, Crisosto, Wiley, & Crisosto, 2005). A digital Brix pocket refractometer measured total soluble solids in °Brix. Each parameter has five replicates.

2.4 Morphological analysis

A scanning electron microscope (JEOL JSM-7600F Field Emission Scanning Electron Microscope (FESEM), Japan) was used to count trichomes and stomata in tomato leaves. A method by Karcz (2009) was applied to prepare the samples. Accordingly, the leaf samples were fixed in 3% glutaraldehyde for 2 hours; then, they were washed with 0.1 M phosphate buffer (pH = 7.2); after that, the samples were fixed using 1–2% osmium tetroxide for two hours and rinsed in 0.1 M phosphate buffer, and then, the dehydration was conducted using consecutive concentrations of ethanol (25/75/95/100/100 %). After that, critical point drying was carried out. Lastly, the specimens were set on metal stubs and coated with gold. The photos were obtained using 20 kV voltages. There were four replicates for each treatment.

2.5 Biochemical analysis

2.5.1 Proline. Proline plays a beneficial role in plants exposed to diverse stress conditions. Besides acting as an excellent osmolyte, it provides three main advantages during stress: an antioxidative defense molecule, a metal chelator and a signaling molecule (Hayat *et al.*, 2012). A protocol of Bates, Waldren and Teare (1973) was applied to determine proline content in tomato leaves. Accordingly, 0.5 g of leaf samples were weighed and extracted using sulphosalicylic acid (3%), the extract (2 mL) was transferred to a test tube, ninhydrin reagent (2 mL) and glacial acetic acid (2 mL) was added. The mixture was boiled for 30 min in a water bath; after cooling the mixture, toluene (6 mL) was added, mixed and separated. The reading was observed at 520 nm, a standard curve was created, and the readings were compared to it; finally, the formula provided by Bates *et al.* (1973) was applied. Four replicates were set for this test.

2.5.2 Gibberellic acid (GA3). GA3 is among plants' most critical growth regulators which promotes their tolerance to drought stress under optimum concentration (Sarwar *et al.*, 2017). The extraction of leaf samples was performed in methanol solvent (70% v/v) following Kelen, Demiralay, Şen, and Alsancak (2004) method. Accordingly, the leaf materials were homogenized with the solvent and stirred overnight at 4°C, then the matrix was filtered, and the methanol was evaporated under vacuum; the obtained aqueous phase was adjusted to pH 8.5; after that, it partitioned with ethyl acetate three times, the obtained aqueous phase was adjusted to pH 2.5, then the solution was partitioned using diethyl ether three times, and passed through sodium sulfate; the diethyl ether phase was evaporated, and the obtained dry material was dissolved in 2 mL of methanol and stored at 4°C. GA3 content was determined using liquid chromatography-tandem mass spectrometry (LC–MS/MS: AB Sciex). Several standards of GA3 (0.001, 0.01, 0.1, 1 mg/L) were prepared, and acetonitrile water (26:74; 30:70%; v/v) was selected as the mobile phase. Three replicates were set for this test.

2.5.3 Chlorophyll measurements. Chlorophyll fluorescence: the ratio of Fv (variable fluorescence) to Fm (maximum fluorescence) represents the quantum efficiency of open photosystem II centers (Maxwell & Johnson, 2000). It was measured in dark-adapted tomato leaves using a plant efficiency analyzer. The adaptation continued for 30 min before measurement (Morales, Abadía, & Abadia, 1991). The microelectrode was positioned vertically during the reading recording. A total of 16 random leaves from each treatment were selected to perform this test; the measurement of chlorophyll fluorescence was a valid and reliable tool for rapid screening drought stress tolerance in other plants (Faraloni *et al.*, 2011; Li, Guo, Michael, Stefania, & Salvatore, 2006).

Chlorophyll contents: chlorophyll *a*, chlorophyll *b* and carotenoids were measured following the protocol of Sumanta, Haque, Nishika, and Suprakash (2014). Briefly, the extraction of tomato leaves was carried out using acetone (80%), the absorption was read by spectrophotometer at 663.2, 646.8 and 470 nm, and the formulas provided by Sumanta *et al.* (2014) were applied to obtain the values of Chl*a*, Chl*b* and carotenoids. Four replicates were set for this test.

2.6 Statistical analysis

Statistical analysis was performed using SPSS software. One-way analysis of variance (ANOVA) with POSTHOC test: least significant difference (LSD) was selected to compare the means of treatments. The significance level was adjusted at 0.05.

3. Results

3.1 Pollen viability and growth characteristics

Pollen viability and growth characteristics of tomato plants are displayed in Table 1. All endophytic fungi treatments (stressed and nonstressed *A. fumigatus* (18.90) (14.18), stressed and non–stressed *A. terreus* (16.36) (16.75), stressed and non–stressed *T. variabilis* (16.54) (15.07) consecutively) and control (17.72%) significantly decreased the pollen sterility of tomatoes compared to drought treatment (25.78%) (Table 1). Also, non–stressed *A. fumigatus* (98.86 cm) significantly increased the root length of the tomato compared to all other treatments, including the control (57.62 cm) and drought (58 cm) (Table 1). Shoot fresh weight was significantly enhanced under the effect of nonstressed *A. fumigatus* (154.4 g) and nonstressed *A. terreus* (139.84 g) compared to the control (77.5 g) and drought stress treatment (78.01 g). Shoot dry weight was significantly increased under nonstressed *A. fumigatus* (24.19 g), *A. terreus* (stressed (23.23 g) and nonstressed (24.59 g)) and stressed *T. variabilis* (22.98 g) compared to the control (14.35 g). Root fresh weight was significantly enhanced by nonstressed *A. terreus* (36.53 g) compared to the control (18.27 g) and drought stress (18.06 g) (Table 1). Similarly, nonstressed *A. terreus* significantly increased root dry weight (4.84 g) compared to the control (2.58 g) and drought stress (2.52 g). The leaf area was significantly enhanced by stressed *T. variabilis* (26.34 cm^2) followed by nonstressed *A. fumigatus* (22.69 cm^2) compared to the control (17.51 cm^2) and drought stress (14.59 cm^2) (Table 1).

3.2 Fruit characteristics

As illustrated in Table 2, the total numbers of fruits were significantly increased by all endophytic fungi treatments under favorable and drought stress conditions compared to drought treatment; the best treatment among them was the stressed *A. terreus*. Specifically,

Table 1. Pollen viability and growth characteristics of tomato plants under the effect of endophytic fungi

Treatments	Pollen sterility (%)	Shoot length (cm)	Root length (cm)	Shoot fresh weight (g)	Root fresh weight (g)	Shoot dry weight (g)	Root dry weight (g)	Leaf area (cm^2)
10P	14.18 ± 2.96b	77 ± 10.13a	98.86 ± 25.29a	154.4 ± 32.72a	25.76 ± 4.25ab	24.19 ± 5.94a	3.63 ± 0.86ab	22.69 ± 4.22ab
D10P	18.90 ± 2.42b	60.7 ± 8.60b	68.57 ± 7.74b	98.94 ± 35.32c	23.23 ± 9.57b	19.79 ± 3.85ab	4.03 ± 1.21ab	19.66 ± 3.75bc
65P	16.75 ± 2.9b	63.6 ± 6.43b	76 ± 30.47b	139.84 ± 40.55ab	36.53 ± 19.28a	24.59 ± 6.56a	4.84 ± 2.97a	21.41 ± 3.39bc
D65P	16.36 ± 2.94b	72.8 ± 20.80ab	75.29 ± 7.28b	84.97 ± 23.49c	26.04 ± 10.13ab	23.23 ± 6.52a	4.29 ± 1.43ab	12.91 ± 1.65d
48P	15.07 ± 2.50b	72.83 ± 6.27ab	73.86 ± 17.79b	105.39 ± 32.58bc	23.78 ± 8.46b	19.68 ± 7.14ab	3.39 ± 1.37ab	20.86 ± 5.66bc
D48P	16.54 ± 0.21b	65.45 ± 7.33ab	74.88 ± 11.69b	102.45 ± 41.73bc	29.32 ± 11.55ab	22.98 ± 9.41a	4.26 ± 2.05ab	26.34 ± 3.09a
W	17.72 ± 1.63b	72.45 ± 10.63ab	57.62 ± 8.76b	77.5 ± 19.90c	18.27 ± 4.78b	14.35 ± 3.76b	2.58 ± 0.80b	17.51 ± 2.43cd
D	25.78 ± 5.45a	71.63 ± 6.39ab	58 ± 14.48b	78.01 ± 19.58c	18.06 ± 4.51b	16.92 ± 5.97ab	2.52 ± 0.94b	14.59 ± 1.62d

Note(s): Values of pollen viability represent the means ± SD, other values represent the means ± 95% confidence limits. Different letters in the same column refers to significant differences according to LSD test ($\alpha = 0.05$)

Table 2.
Fruit characteristics of tomato plants under the effect of endophytic fungi

Treatments	Total number of fruits	Number of ripe fruits	Number of mature fruits	Fruit weight (g)	Fruit width (cm)	Fruit length (cm)	pH	Titratable acidity (%)	Total soluble solids (°Brix)
10P	5.11 ± 2.38bc	1 ± 0.86d	4.11 ± 1.98ab	33.37 ± 4.77b	3.19 ± 0.36d	3.49 ± 0.32c	4.66 ± 0.14b	0.39 ± 0.06a	6.28 ± 0.76b
D10P	5 ± 1.47bc	1.9 ± 1.37bcd	3.1 ± 1.04bcd	47.53 ± 14.58a	4.06 ± 0.96abc	3.78 ± 0.38abc	4.7 ± 0.23b	0.41 ± 0.12a	6.6 ± 0.77ab
65P	5.3 ± 2.52bc	3.5 ± 1.76a	1.8 ± 1.00cde	45.7 ± 7.59ab	4.58 ± 0.14a	4.1 ± 0.22ab	4.72 ± 0.24b	0.41 ± 0.09a	6.54 ± 0.33ab
D65P	9.1 ± 2.14a	3.2 ± 1.00ab	5.9 ± 1.49a	44.64±8ab	3.68 ± 0.46bcd	4.22 ± 0.43a	4.68 ± 0.24b	0.4 ± 0.11a	6.18 ± 0.97b
48P	6.2 ± 2.63b	2.7 ± 0.89ab	3.5 ± 2.44bc	50.51 ± 10.39a	4.51 ± 0.41a	4.05 ± 0.30ab	4.72 ± 0.20b	0.4 ± 0.04a	6.54 ± 0.50ab
D48P	5.11 ± 1.18bc	3.56 ± 1.16a	1.56 ± 0.56de	40.25 ± 8.75ab	4.33 ± 0.38ab	3.78 ± 0.33abc	4.72 ± 0.10b	0.42 ± 0.05a	6.74 ± 0.64ab
W	3.5 ± 0.84cd	2.6 ± 0.84abc	0.9 ± 0.86e	40.91 ± 12.93ab	3.53 ± 0.41cd	3.86 ± 0.66abc	5.12 ± 0.16a	0.31 ± 0.04b	5.07 ± 0.10c
D	2.44 ± 1.64d	1.11 ± 0.81d	1.33 ± 1.2de	33.71 ± 16.53b	3.14 ± 0.82d	3.6 ± 0.66bc	5.16 ± 0.17a	0.44 ± 0.02a	7.16 ± 1.87a

Note(s): The values represent the means ± 95% confidence limits. Different letters in the same column refers to significant differences according to LSD test ($\alpha = 0.05$)

A. terreus and *T. variabilis* fungal treatments (stressed and nonstressed) and the control significantly increased the number of ripe fruits compared to drought stress treatment. The numbers of mature fruits were significantly enhanced by stressed *A. terreus*, nonstressed *A. fumigatus* and nonstressed *T. variabilis* treatments compared to the control and drought stress treatment (Table 2). Fruit weight was significantly increased through the inoculation by stressed *A. fumigatus* (47.53 g) and nonstressed *T. variabilis* (50.51 g) compared to drought stress treatment (33.71 g). Also, fruit width was significantly increased through the inoculation by nonstressed *A. terreus* (4.58 cm), stressed *A. fumigatus* (4.06 cm), and *T. variabilis* (stressed (4.33 cm) and nonstressed (4.51 cm)) compared to the drought treatment (3.14 cm). Moreover, stressed *A. terreus* significantly increased the length of tomato fruits (4.22 cm) compared to the drought treatment (3.6 cm) (Table 2). pH values were significantly decreased under the fungal treatments normally and under stress conditions compared to the control and drought stress treatment. However, titratable acidity was significantly increased by all fungal treatments (stressed and nonstressed) and drought treatment compared to the control. Total soluble solids were significantly increased under the effects of all fungal treatments (stressed and nonstressed) and drought treatment compared to the control (Table 2).

3.3 Morphological analysis

The morphological characteristics of tomato leaves are shown in Table 3 and Figure 1. Trichomes' numbers (per mm^2) were significantly increased under all fungal treatments (stressed and nonstressed) compared to the control. Also, most of the fungal treatments: (*A. fumigatus* (stressed (195.25) and nonstressed (117.75)), *A. terreus* (stressed (184.5) and nonstressed (207)), and stressed *T. variabilis* (337)) significantly increased the numbers of trichomes compared to drought treatment (147.6). Moreover, under drought stress, *A. fumigatus* and *T. variabilis* significantly increased number of trichomes compared to nonstress treatments. Similarly, drought treatment significantly increased number of trichomes (147.6) compared to the control (77) (Table 3 and Figure 1). The number of stomata (per mm^2) was significantly increased under all the fungal treatments (stressed and non–stressed) and drought treatment compared to the control. Moreover, the maximum number of stomata was observed under nonstressed *A. terreus* treatment (45.4) (Table 3).

3.4 Biochemical analysis

The biochemical characteristics of tomato plants are displayed in Table 4. The highest proline concentration was found under drought stress treatment; proline concentrations significantly increased under all stressed fungal treatments compared to the control and

Treatments	Trichomes number (per mm^2)	Stomata number (per mm^2)
10P	117.75 ± 4.11d	28.5 ± 8.7b
D10P	195.25 ± 20.76b	26.5 ± 3.21b
65P	207 ± 8b	45.4 ± 5.22a
D65P	184.5 ± 14.36b	24.8 ± 4.32b
48P	124.67 ± 12.1cd	29 ± 6.23b
D48P	337 ± 19.52a	26.6 ± 4.77b
W	77 ± 10.12e	16.83 ± 3.97c
D	147.6 ± 35.9c	30.75 ± 7.93b

Note(s): The values represent the means ± SD. Different letters in the same column refers to significant differences according to LSD test ($\alpha = 0.05$)

Table 3. Morphological characteristics of tomato leaves under the effect of endophytic fungi

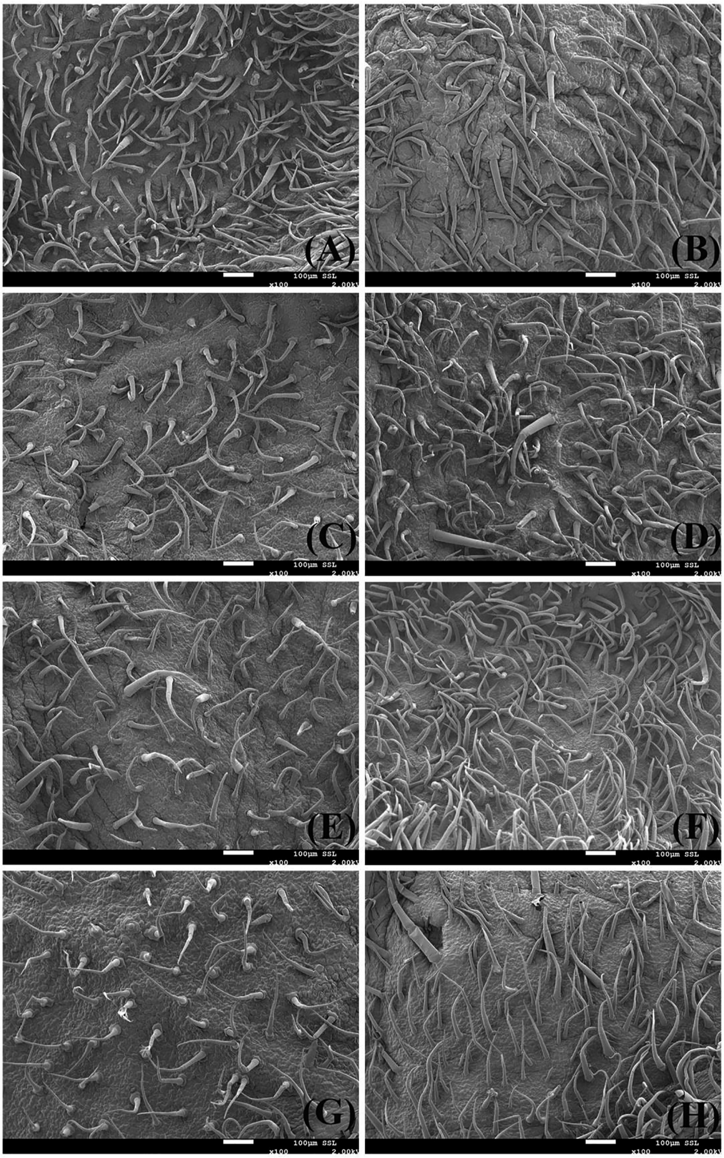

Figure 1.
Trichomes of tomato leaves under the effect of endophytic fungi: 65p (A), D65P (B), 10P (C), D10P (D), 48P (E), D48P (F), W (G), D (H)

nonstressed fungal treatments. However, stressed *A. fumigatus* and stressed *A. terreus* treatments significantly had a higher amount of proline than stressed *T. variabilis* treatment (Table 4). GA3 concentrations were significantly enhanced under *A. fumigatus* (stressed (0.6 ppm) and nonstressed (0.6 ppm)) and *A. terreus* (stressed (0.6 ppm) and nonstressed (0.45 ppm)) treatments compared to the control (0.12 ppm) and drought treatment (0.12 ppm) (Table 4). Chlorophyll fluorescence significantly increased under the nonstressed *T. variabilis* treatment (0.83) and the control (0.83) compared to the drought treatment (0.79) (Table 4).

Table 4. Biochemical characteristics of tomato plants under the effect of endophytic fungi

Treatments	Proline content (ppm)	Gibberellic acid content (ppm)	Chlorophyll fluorescence	Chlorophyll *a* content (μg/mL)	Chlorophyll *b* content (μg/mL)	Carotenoids content (μg/mL)
10P	0.22 ± 0.15d	0.6 ± 0a	0.81 ± 0.04abc	3.93 ± 0.83ab	1.79 ± 0.43b	288.58 ± 48.93c
D10P	33.4 ± 14.95b	0.6 ± 0a	0.8 ± 0.04abc	5.27 ± 1.41a	2.48 ± 0.67a	415.31 ± 89.12a
65P	0.76 ± 0.24d	0.45 ± 0.3ab	0.81 ± 0.05abc	4.24 ± 0.12ab	1.85 ± 0.16ab	311.27 ± 14.68bc
D65P	36.32 ± 14.70b	0.6 ± 0a	0.81 ± 0.07abc	5.19 ± 1.25a	2.43 ± 0.52a	400.53 ± 91.44ab
48P	0.12 ± 0.00d	0 ± 0c	0.83 ± 0.02a	4.21 ± 1.03ab	1.87 ± 0.50ab	312.74 ± 76.05bc
D48P	22.82 ± 8.50c	0.2 ± 0.35bc	0.79 ± 0.06bc	4.33 ± 0.28ab	1.9 ± 0.21ab	319.16 ± 63.00abc
W	1.3 ± 0.84d	0.12 ± 0.27c	0.83 ± 0.01ab	4.38 ± 0.92ab	2.08 ± 0.45ab	342.06 ± 65.57abc
D	48.47 ± 9.35a	0.12 ± 0.27c	0.79 ± 0.04c	3.75 ± 0.75b	1.64 ± 0.47b	272.7 ± 75.93c

Note(s): The values represent the means ± SD. Different letters in the same column refers to significant differences according to LSD test ($\alpha = 0.05$)

Chlorophyll *a*, chlorophyll *b*, and carotenoids contents were significantly increased under stressed *A. fumigatus* and stressed *A. terreus* treatments (Table 4).

4. Discussion

The current study found that the inoculation with endophytic fungi induced multiple responses in tomato plants; they enhanced several characteristics under stressed and unstressed conditions.

The expansion of drought in many parts of the world is a catastrophic problem that has destructive impacts at several levels, the most important of which is its effect on plant growth, reproduction and production. Hence, finding cheap and eco-friendly strategies that improve plant tolerance to drought stress is an essential destination. Currently, we investigated the role of desert endophytic fungi, *A. fumigatus*, *A. terreus* and *T. variabilis*, in enhancing the drought tolerance of tomato plants. These endophytes can achieve that purpose by enhancing several characteristics under drought stress.

Pollen viability is an effective indicator that measures a plant's ability to develop into seed and fruit; drought stress decreased pollen viability of tomatoes and other crops according to our findings and previous studies (Hu *et al.*, 2020); nevertheless, this was promoted by our fungal treatments under stressed and nonstressed conditions. Similarly, *Talaromyces omanensis* enhanced the pollen viability of tomatoes under natural and drought-stress conditions (Halo *et al.*, 2020). Also, the inoculation by *Piriformospora indica* fungus enhanced the pollen viability of *Cyclamen persicum* (Ghanem, Ewald, Zerche, & Hennig, 2014). Most of our endophytic fungi increased the levels of GA3 in tomato leaves, which elucidates the valuable role in improving pollen viability (Li, Tian, Guo, Luo, & Li, 2021).

The current fungal treatments partly enhanced growth characteristics. The best treatment was nonstressed *A. fumigatus* which increased shoot length, root length, shoot fresh weight, shoot dry weight and leaf area. The next one was nonstressed *A. terreus* which enhanced the shoot fresh weight, root fresh weight and shoot dry weight of tomatoes. Several endophytic fungi had the ability to improve growth features, including a desert-adapted endophytic fungus, *Serendipita indica*, which promoted shoot and root growth of stressed and non–stressed tomato plants (Ghabooli & Kaboosi, 2022). Similarly, *Aspergillus flavus* and *A. terreus* fungi promoted the growth features of tomatoes (Abdel-Motaal, Kamel, El-Zayat, & Abou-Ellail, 2020; Yoo, Shin, Won, Song, & Sang, 2018).

Drought stress decreased the yields of tomatoes and other essential crops; the current results proved this trend. Various mechanisms were conducted to mitigate that expanded disaster. In particular, inoculation with endophytic microbes provided a safe and sustainable approach (Harman & Uphoff, 2019). As proof, an endophytic fungus Ampelomyces sp. promoted the yield of tomatoes under drought stress (Morsy *et al.*, 2020); the yield enhancement was also detected under nonstressed status, as clarified in a Flores *et al.* (2020) study that applied *Bacillus thuringiensis* endophyte to enhance the growth and yield of *Cucumis sativus*.

Similarly, the current study clarified that all endophytic fungi treatments improved the total yield of tomatoes under normal and stressful conditions. Moreover, the number of ripe fruits was enhanced by the inoculation with *A. terreus* and *T. variabilis* in both stressed and nonstressed conditions; however, *A. fumigatus* and *T. variabilis* enhanced the number of mature fruits under normal conditions.

Endophytic fungi improve fruit characteristics, such as *Piriformospora indica*, which enhanced tomato fruit weight and *Trichoderma koningiopsis*, which enhanced the fruit weight of *Ananas comosus* (Trocoli, Monteiro, Santos, & De Souza, 2017). Moreover, an endophytic *Talaromyces omanensis* increased the width of tomato fruits under favorable and drought-stress conditions (Halo *et al.*, 2020).

Similarly, our endophytic fungi enhanced some fruit features, including fruit weight and size. Nonstressed *T. variabilis* and stressed *A. fumigatus* enhanced the weight of tomato fruits. Also, most fungal treatments showed increased tomato width (*T. variabilis,* nonstressed *A. terreus* and stressed *A. fumigatus*). However, only one treatment (stressed *A. terreus*) increased the length of tomato fruits.

In the current study, titratable acidity and total soluble solids were enhanced under all fungal and drought treatments. Similarly, drought stress increased these fruit qualities according to Rad, Asghari, and Hasan's (2015) study. Moreover, the inoculation by endophytes enhanced fruit soluble sugar of apple (Rho, Van Epps, Kim, & Doty, 2020), as well, *Diversispora versiformis* fungus improved orange fruit quality, including total soluble solids and mineral element contents of their hosts (Cheng *et al.*, 2022).

The applied endophytic fungi reduced pH values under stressed and unstressed treatments; similarly, the pH values of strawberry were decreased under the bacterial inoculation of *Pseudomonas* sp. (Todeschini *et al.*, 2018). Malic and citric acids contents mainly effect pH values; numerous factors control the accumulation of these two acids in fruit cells, including the interactions between metabolism and vacuolar storage, sink ratio, water supply, mineral nutrition and temperature (Etienne, Génard, Lobit, Mbeguié-A-Mbéguié, & Bugaud, 2013), consequently, the applied microbes likely control one or more of these influential factors which resulted in pH reduction.

Numerous mechanisms are utilized by endophytes to enhance their host growth, yield and fruit quality under favorable and drought stress conditions, involving promoting photosynthetic activity, phytohormones production, enhancing nutrient absorption, synthesis of osmolytes, scavenging of reactive oxygen species and altering gene expression (Lu, Wei, Lou, Shu, & Chen, 2021); currently, proline, GA3, chlorophyll measurements and trichome density clarified some aspects of the provided role as follows:

According to the present study, all fungal treatments and drought treatment increased the number of trichomes. Similarly, studies of Muthukumaran and Anusuya (2018) and del Rosario Cappellari, Santoro, Schmidt, Gershenzon, and Banchio (2019) found that the microbial inoculation increased trichome density of *Solanum lycopersicum* and *Mentha piperita* plants. In addition, the present study showed that the stressed fungal treatments significantly had greater trichomes than the drought treatment. This finding represents a real benefit for the plants under drought conditions because the trichomes have an influential role in protecting drought-stressed plants through preserving higher levels of water, absorbing dew deposits, reflecting solar radiations and enhancing photosynthetic performance (Ning *et al.*, 2016). Thus, our endophytic fungi efficiently adapted tomato plants to drought stress through the significant increase of trichomes density; previous studies illustrated that gibberellins and jasmonates stimulate trichomes formation in multiple stressed plants (Castro-Camba, Sánchez, Vidal, & Vielba, 2022; Hua *et al.*, 2022); hence, it is probably because endophytes elevated the density of trichomes through GA3 secretion.

The current study found that stomata numbers increased in the fungal-treated and drought-stressed plants; nonstressed *A. terreus* recorded the highest number of stomata. However, the inoculation by an endophytic fungus *Trichoderma asperellum* reduced the stomata density of *Theobroma cacao* (Rosmana, Nasaruddin, Hendarto, Hakkar, & Agriansyah, 2016).

Although the reduction in stomata number feature is more tolerant to drought stress (Caine *et al.*, 2019), the remarkable rise of trichomes density by our endophytes maintains a high level of water even though the number of stomata was more.

The current study showed that the highest concentration of proline was observed under the drought treatment, followed by drought-stressed treatments of endophytic fungi compared to the control and nonstressed treatments. Similarly, tomato plants that were inoculated with an endophytic fungus *Talaromyces omanensis* accumulated lower concentrations of proline under drought stress than non-inoculated stressed plants (Halo *et al.*, 2020); also, *Trichoderma harzianum* endophyte caused the same impact on their rice host (Shukla, Awasthi, Rawat, & Kumar, 2012). The fungal-inoculated plants were less affected by drought stress than noninoculated stressed plants; this most likely explains the decrease in proline content in their leaves (Zou, Wu, Huang, Ni, & He, 2013). In the present study, the plants inoculated with *A. fumigatus* and *A. terreus* concentrated higher amounts of GA3 under stressed and non–stressed conditions. Some studies reported that the endophytic fungi could increase the levels of GA3 and other phytohormones in their unstressed host plants such as *A. fumigatus* and *Fusarium proliferatum* (Bilal *et al.*, 2018) and under drought stress conditions such as *Trichoderma harzianum* (Mona *et al.*, 2017).

The improvement of growth characteristics of crops by endophytes was associated with improving phytohormones content (Verma *et al.*, 2021). Similarly, the current study found that *A. fumigatus* and *A. terreus* accumulated a higher amount of GA3, which stimulated cell elongation and division; thus, yield characteristics and several growth features of tomato plants were enhanced. According to the current study, nonstressed *T. variabilis* and the control increased the Fv/Fm ratio and enhanced chlorophyll fluorescence of tomato leaves; chlorophyll contents and carotenoids were enhanced under stressed *A. fumigatus* and stressed *A. terreus*, this impact probably explicated through enhancing chlorophyll synthesis by promoting its components absorption via the applied endophytes. Several endophytes were reported to enhance chlorophyll fluorescence and chlorophyll contents in their hosts, such as *Piriformospora indica* (Shahabivand, Parvaneh, & Aliloo, 2017). Also, an endophytic *Exophiala pisciphila* enhanced the chlorophyll fluorescence of *Sorghum bicolor* under drought-stress conditions (Zhang *et al.*, 2017).

5. Conclusion

Abiotic stress management using endophytes is a promising and sustainable field mitigating mounting climate change risks; therefore, they have been increasingly studied in the last two decades. Distinctively, stress-adapted endophytes attracted growing research attention as they are more efficient in achieving the desired aims. Currently, the drought-adapted endophytes, *A. fumigatus*, *A. terreus* and *T. variabilis* provide several benefits to their tomato hosts under drought stress. They significantly promoted pollen viability, trichome and stomata density and the yield of tomatoes under stressed and nonstressed conditions. Moreover, all of them enhanced tomato fruit quality involving total soluble solids and titratable acidity compared to the control; also, they reduced the pH values of tomato fruits; individually, the best endophytic fungus that enhanced growth characteristics under normal conditions was *A. fumigatus* followed by *A. terreus*; however, fruit characteristics were enhanced by *T. variabilis*.

Overall, adding the present endophytic fungi to crop plants provides impressive benefits in normal and stressed agricultural systems, particularly enhancing yield and fruit quality.

These results were partly interpreted through the present investigated measurements: GA3 concentrations, chlorophyll and carotenoids contents, chlorophyll fluorescence and trichomes formations. Since our study introduced some elucidated mechanisms provided by drought-adapted endophytic fungi, it is recommended to investigate other mechanisms of stress-adapted endophytes on the molecular, biochemical and anatomical levels, such as phytohormone synthesis, nutrient absorption, phosphate solubilization and antioxidant enzymes activity, inducing systemic resistance and modulating anatomical composition.

References

Abdel-Motaal, F., Kamel, N., El-Zayat, S., & Abou-Ellail, M. (2020). Early blight suppression and plant growth promotion potential of the endophyte *Aspergillus flavus* in tomato plant. *Annals of Agricultural Sciences*, *65*(2), 117–123.

Abdul-Baki, A. A. (1992). Determination of pollen viability in tomatoes. *Journal of the American Society for Horticultural Science*, *117*(3), 473–476.

Ali, Z., Rai, S., Jan, S., & Raina, K. (2022). An assessment on CRISPR Cas as a novel asset in mitigating drought stress. *Genetic Resources and Crop Evolution*, *69*(6), 2011–2027.

Anderson, R., Bayer, P. E., & Edwards, D. (2020). Climate change and the need for agricultural adaptation. *Current Opinion in Plant Biology*, *56*, 197–202.

Azeem, M., Haider, M. Z., Javed, S., Saleem, M. H., & Alatawi, A. (2022). Drought stress amelioration in maize (*Zea mays* L.) by inoculation of *Bacillus* spp. strains under sterile soil conditions. *Agriculture*, *12*(1), 50.

Bates, L. S., Waldren, R. P., & Teare, I. (1973). Rapid determination of free proline for water-stress studies. *Plant and Soil*, *39*(1), 205–207.

Beecher, G. R. (1998). Nutrient content of tomatoes and tomato products. *Proceedings of the Society for Experimental Biology and Medicine*, *218*(2), 98–100.

Bilal, L., Asaf, S., Hamayun, M., Gul, H., Iqbal, A., Ullah, I., . . . Hussain, A. (2018). Plant growth promoting endophytic fungi *Asprgillus fumigatus* TS1 and *Fusarium proliferatum* BRL1 produce gibberellins and regulates plant endogenous hormones. *Symbiosis*, *76*(2), 117–127.

Bilal, S., Shahzad, R., Imran, M., Jan, R., Kim, K. M., & Lee, I. -J. (2020). Synergistic association of endophytic fungi enhances *Glycine max* L. resilience to combined abiotic stresses: Heavy metals, high temperature and drought stress. *Industrial Crops and Products*, *143*, 111931.

Caine, R. S., Yin, X., Sloan, J., Harrison, E. L., Mohammed, U., Fulton, T., . . . Coe, R. A. (2019). Rice with reduced stomatal density conserves water and has improved drought tolerance under future climate conditions. *New Phytologist*, *221*(1), 371–384.

Castro-Camba, R., Sánchez, C., Vidal, N., & Vielba, J. M. (2022). Plant development and crop yield: The role of gibberellins. *Plants*, *11*(19), 2650.

Chen, H., Liang, Z., Liu, Y., Jiang, Q., & Xie, S. (2018). Effects of drought and flood on crop production in China across 1949–2015: Spatial heterogeneity analysis with Bayesian hierarchical modeling. *Natural Hazards*, *92*(1), 525–541.

Cheng, X. -F., Xie, M. -M., Li, Y., Liu, B. -Y., Liu, C. -Y., Wu, Q. -S., & Kuča, K. (2022). Effects of field inoculation with arbuscular mycorrhizal fungi and endophytic fungi on fruit quality and soil properties of Newhall navel orange. *Applied Soil Ecology*, *170*, 104308.

Cuc, D., Phuong, P., Loan, N., Cuong, N., Ngoan, N., Phuc, N., . . . Trung, K. (2021). Integration of traditional and molecular breeding to improve drought tolerance of groundnut. *Advanced Studies in Biology*, *13*(1), 29–36.

Cui, J., Shao, G., Lu, J., Keabetswe, L., & Hoogenboom, G. (2020). Yield, quality and drought sensitivity of tomato to water deficit during different growth stages. *Scientia Agricola*, *77*(2), e20180390.

del Rosario Cappellari, L., Santoro, M. V., Schmidt, A., Gershenzon, J., & Banchio, E. (2019). Induction of essential oil production in Mentha x piperita by plant growth promoting bacteria was correlated with an increase in jasmonate and salicylate levels and a higher density of glandular trichomes. *Plant Physiology and Biochemistry*, *141*, 142–153.

Dinesh, R., Srinivasan, V., TE, S., Anandaraj, M., & Srambikkal, H. (2017). Endophytic actinobacteria: Diversity, secondary metabolism and mechanisms to unsilence biosynthetic gene clusters. *Critical Reviews in Microbiology*, *43*(5), 546–566.

El-Sayed, A. S., Shindia, A. A., Ali, G. S., Yassin, M. A., Hussein, H., Awad, S. A., & Ammar, H. A. (2021). Production and bioprocess optimization of antitumor Epothilone B analogue from *Aspergillus fumigatus*, endophyte of *Catharanthus roseus*, with response surface methodology. *Enzyme and Microbial Technology*, *143*, 109718.

Etienne, A., Génard, M., Lobit, P., Mbeguié-A-Mbéguié, D., & Bugaud, C. (2013). What controls fleshy fruit acidity? A review of malate and citrate accumulation in fruit cells. *Journal of Experimental Botany*, *64*(6), 1451–1469.

Faraloni, C., Cutino, I., Petruccelli, R., Leva, A., Lazzeri, S., & Torzillo, G. (2011). Chlorophyll fluorescence technique as a rapid tool for in vitro screening of olive cultivars (*Olea europaea* L.) tolerant to drought stress. *Environmental and Experimental Botany*, *73*, 49–56.

Fernandez-Munoz, R., Gonzalez-Fernandez, J., & Cuartero, J. (1994). Methods for testing the fertility of tomato pollen formed at low temperature. *Journal of Horticultural Science*, *69*(6), 1083–1088.

Flores, A., Diaz-Zamora, J. T., del Carmen Orozco-Mosqueda, M., Chávez, A., de los Santos-Villalobos, S., Valencia-Cantero, E., & Santoyo, G. (2020). Bridging genomics and field research: Draft genome sequence of *Bacillus thuringiensis* CR71, an endophytic bacterium that promotes plant growth and fruit yield in *Cucumis sativus* L. *3 Biotech*, *10*(5), 220.

Garner, D., Crisosto, C., Wiley, P., & Crisosto, G. (2005). *Measurement of pH and titratable acidity. Quality Evaluation Methodology*. Kearney Agricultural Center. Available from: file:///C:/Users/user/Downloads/Measurement_of_pH_and_Titratable_Acidity.pdf

Ghabooli, M., & Kaboosi, E. (2022). Alleviation of the adverse effects of drought stress using a desert adapted endophytic fungus and glucose in tomato. *Rhizosphere*, *21*, 100481.

Ghanem, G., Ewald, A., Zerche, S., & Hennig, F. (2014). Effect of root colonization with *Piriformospora indica* and phosphate availability on the growth and reproductive biology of a *Cyclamen persicum* cultivar. *Scientia Horticulturae*, *172*, 233–241.

Halo, B. A., Al-Yahyai, R., & Al-Sadi, A. M. (2018). *Aspergillus terreus* inhibits growth and induces morphological abnormalities in *Pythium aphanidermatum* and suppresses *Pythium*-induced damping-off of cucumber. *Frontiers in Microbiology*, *9*, 95.

Halo, B., Al-Yahyai, R. A., & Al-Sadi, A. M. (2020). An endophytic *Talaromyces omanensis* enhances reproductive, physiological and anatomical characteristics of drought-stressed tomato. *Journal of Plant Physiology*, *249*, 153163.

Halo, B. A., Al-Yahyai, R. A., Maharachchikumbura, S. S. N., & Al-Sadi, A. M. (2019). *Talaromyces variabilis* interferes with *Pythium aphanidermatum* growth and suppresses *Pythium*-induced damping-off of cucumbers and tomatoes. *Scientific Reports*, *9*(1), 11255. doi: 10.1038/s41598-019-47736-x.

Harman, G. E., & Uphoff, N. (2019). Symbiotic root-endophytic soil microbes improve crop productivity and provide environmental benefits. *Scientifica*, *2019*, 9106395.

Hayat, S., Hayat, Q., Alyemeni, M. N., Wani, A. S., Pichtel, J., & Ahmad, A. (2012). Role of proline under changing environments: A review. *Plant Signaling and Behavior*, *7*(11), 1456–1466.

Hu, W., Huang, Y., Bai, H., Liu, Y., Wang, S., & Zhou, Z. (2020). Influence of drought stress on pistil physiology and reproductive success of two *Gossypium hirsutum* cultivars differing in drought tolerance. *Physiologia Plantarum*, *168*(4), 909–920.

Hua, B., Chang, J., Han, X., Xu, Z., Hu, S., Li, S., . . . Wu, S. (2022). H and HL synergistically regulate jasmonate-triggered trichome formation in tomato. *Horticulture Research*, *9*, uhab080.

Hubbard, M., Germida, J., & Vujanovic, V. (2014). Fungal endophytes enhance wheat heat and drought tolerance in terms of grain yield and second-generation seed viability. *Journal of Applied Microbiology*, *116*(1), 109–122.

Hussein, M. E., Mohamed, O. G., El-Fishawy, A. M., El-Askary, H. I., El-Senousy, A. S., El-Beih, A. A., . . . Tripathi, A. (2022). Identification of antibacterial metabolites from endophytic fungus *Aspergillus fumigatus*, isolated from *Albizia lucidior* leaves (Fabaceae), utilizing metabolomic and molecular docking techniques. *Molecules*, *27*(3), 1117.

Ilyas, M., Nisar, M., Khan, N., Hazrat, A., Khan, A. H., Hayat, K., and . . . Ullah, A. (2020). Drought tolerance strategies in plants: A mechanistic approach. *Journal of Plant Growth Regulation*, *40*, 926–944.

Jehanzaib, M., & Kim, T. -W. (2020). Exploring the influence of climate change-induced drought propagation on wetlands. *Ecological Engineering*, *149*, 105799.

Karcz, J. (2009). *Scanning electron microscopy in biology*. Laboratory of Scanning Electron Miscroscopy, Faculty of Biology and Environmental Protection, University of Silesia.

Kelen, M., Demiralay, E. C., Şen, S., & Alsancak, G. Ö. (2004). Separation of abscisic acid, indole-3-acetic acid, gibberellic acid in 99 R (*Vitis berlandieri* x *Vitis rupestris*) and rose oil (*Rosa damascena* Mill.) by reversed phase liquid chromatography. *Turkish Journal of Chemistry*, *28*(5), 603–610.

Khan, A. L., Hamayun, M., Kim, Y. -H., Kang, S. -M., Lee, J. -H., & Lee, I. -J. (2011). Gibberellins producing endophytic *Aspergillus fumigatus* sp. LH02 influenced endogenous phytohormonal levels, isoflavonoids production and plant growth in salinity stress. *Process Biochemistry*, *46*(2), 440–447.

Khan, A. R., Ullah, I., Waqas, M., Shahzad, R., Hong, S.-J., Park, G. -S., . . . Shin, J. -H. (2015). Plant growth-promoting potential of endophytic fungi isolated from *Solanum nigrum* leaves. *World Journal of Microbiology and Biotechnology*, *31*(9), 1461–1466.

Khare, E., Mishra, J., & Arora, N. K. (2018). Multifaceted interactions between endophytes and plant: Developments and prospects. *Frontiers in Microbiology*, *9*, 2732.

Khushdil, F., Jan, F. G., Jan, G., Hamayun, M., Iqbal, A., Hussain, A., & Bibi, N. (2019). Salt stress alleviation in *Pennisetum glaucum* through secondary metabolites modulation by *Aspergillus terreus*. *Plant Physiology and Biochemistry*, *144*, 127–134.

Li, R. -H., Guo, P. -G., Michael, B., Stefania, G., & Salvatore, C. (2006). Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. *Agricultural Sciences in China*, *5*(10), 751–757.

Li, P., Tian, J., Guo, C., Luo, S., & Li, J. (2021). Interaction of gibberellin and other hormones in almond anthers: Phenotypic and physiological changes and transcriptomic reprogramming. *Horticulture Research*, *8*, 94.

Lu, H., Wei, T., Lou, H., Shu, X., & Chen, Q. (2021). A critical review on communication mechanism within plant-endophytic fungi interactions to cope with biotic and abiotic stresses. *Journal of Fungi*, *7*(9), 719.

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence—a practical guide. *Journal of Experimental Botany*, *51*(345), 659–668.

Moghaddam, M. S. H., Safaie, N., Soltani, J., & Hagh-Doust, N. (2021). Desert-adapted fungal endophytes induce salinity and drought stress resistance in model crops. *Plant Physiology and Biochemistry*, *160*, 225–238.

Molina-Montenegro, M. A., Oses, R., Torres-Díaz, C., Atala, C., Zurita-Silva, A., & Ruiz-Lara, S. (2016). Root-endophytes improve the ecophysiological performance and production of an agricultural species under drought condition. *AoB Plants*, *8*, plw062.

Mona, S. A., Hashem, A., Abd_Allah, E. F., Alqarawi, A. A., Soliman, D. W. K., Wirth, S., & Egamberdieva, D. (2017). Increased resistance of drought by *Trichoderma harzianum* fungal treatment correlates with increased secondary metabolites and proline content. *Journal of Integrative Agriculture*, *16*(8), 1751–1757.

Morales, F., Abadía, A., & Abadia, J. (1991). Chlorophyll fluorescence and photon yield of oxygen evolution in iron-deficient sugar beet (*Beta vulgaris* L.) leaves. *Plant Physiology*, *97*(3), 886–893.

Morsy, M., Cleckler, B., & Armuelles-Millican, H. (2020). Fungal endophytes promote tomato growth and enhance drought and salt tolerance. *Plants*, *9*(7), 877.

Muscolo, A., Sidari, M., Anastasi, U., Santonoceto, C., & Maggio, A. (2014). Effect of PEG-induced drought stress on seed germination of four lentil genotypes. *Journal of Plant Interactions*, *9*(1), 354–363.

Muthukumaran, N., & Anusuya, R. (2018). Influence of microbial inoculants on trichomes in tomato against fruit worm. *International Journal of Current Research in Life Sciences*, *7*(4), 1449–1451.

Nataraja, K. N., Dhanyalakshmi, K., Govind, G., & Oelmüller, R. (2022). Activation of drought tolerant traits in crops: Endophytes as elicitors. *Plant Signaling and Behavior*, *17*(1), 2120300.

Nazar, Z., Akram, N. A., Saleem, M. H., Ashraf, M., Ahmed, S., Ali, S., . . . Alyemeni, M. N. (2020). Glycinebetaine-induced alteration in gaseous exchange capacity and osmoprotective phenomena in safflower (*Carthamus tinctorius* L.) under water deficit conditions. *Sustainability*, *12*(24), 10649.

Ning, P., Wang, J., Zhou, Y., Gao, L., Wang, J., & Gong, C. (2016). Adaptional evolution of trichome in *Caragana korshinskii* to natural drought stress on the Loess Plateau, China. *Ecology and Evolution*, *6*(11), 3786–3795.

Parry, M. L. (2019). *Climate change and world agriculture*. London: Routledge, Earthscan Publications.

Rad, M. H., Asghari, M. R., & Hasan, M. (2015). Morphological, chemical and biochemical response to drought stress in pomegranate (*Punica granatum* l.) fruit. *International Journal of Biology, Pharmacy and Allied Sciences*, *4*(12), 64–78.

Ray, R. L., Fares, A., & Risch, E. (2018). Effects of drought on crop production and cropping areas in Texas. *Agricultural and Environmental Letters*, *3*(1), 1–5.

Rho, H., Van Epps, V., Kim, S. -H., & Doty, S. L. (2020). Endophytes increased fruit quality with higher soluble sugar production in honeycrisp apple (*Malus pumila*). *Microorganisms*, *8*(5), 699.

Rosmana, A., Nasaruddin, N., Hendarto, H., Hakkar, A. A., & Agriansyah, N. (2016). Endophytic association of *Trichoderma asperellum* within *Theobroma cacao* suppresses vascular streak dieback incidence and promotes side graft growth. *Mycobiology*, *44*(3), 180–186.

Sadeghi, F., Samsampour, D., Seyahooei, M. A., Bagheri, A., & Soltani, J. (2020). Fungal endophytes alleviate drought-induced oxidative stress in Mandarin (*Citrus reticulata* L.): Toward regulating the ascorbate–glutathione cycle. *Scientia Horticulturae*, *261*, 108991.

Sarwar, N., Farooq, O., Mubeen, K., Wasaya, A., Nouman, W., Zafar Ali, M., & Shehzad, M. (2017). Exogenous application of gibberellic acid improves the maize crop productivity under scarce and sufficient soil moisture condition. *Cercetari Agronomice in Moldova*, *4*(172), 65–73.

Shahabivand, S., Parvaneh, A., & Aliloo, A. A. (2017). Root endophytic fungus *Piriformospora indica* affected growth, cadmium partitioning and chlorophyll fluorescence of sunflower under cadmium toxicity. *Ecotoxicology and Environmental Safety*, *145*, 496–502.

Shukla, N., Awasthi, R., Rawat, L., & Kumar, J. (2012). Biochemical and physiological responses of rice (*Oryza sativa* L.) as influenced by *Trichoderma harzianum* under drought stress. *Plant Physiology and Biochemistry*, *54*, 78–88.

Sumanta, N., Haque, C. I., Nishika, J., & Suprakash, R. (2014). Spectrophotometric analysis of chlorophylls and carotenoids from commonly grown fern species by using various extracting solvents. *Research Journal of Chemical Sciences*, *2231*, 606X.

Todeschini, V., AitLahmidi, N., Mazzucco, E., Marsano, F., Gosetti, F., Robotti, E., … Marengo, E. (2018). Impact of beneficial microorganisms on strawberry growth, fruit production, nutritional quality, and volatilome. *Frontiers in Plant Science*, *9*, 1611.

Trocoli, R., Monteiro, F., Santos, P., & De Souza, J. (2017). Field applications of *Trichoderma* reduce pineapple fusariosis severity and increase fruit weight. *Journal of Plant Pathology*, *99*(1), 225–228.

Verma, H., Kumar, D., Kumar, V., Kumari, M., Singh, S. K., Sharma, V. K., … Kumar, A. (2021). The potential application of endophytes in management of stress from drought and salinity in crop plants. *Microorganisms*, *9*(8), 1729.

Westengen, O. T., & Brysting, A. K. (2014). Crop adaptation to climate change in the semi-arid zone in Tanzania: The role of genetic resources and seed systems. *Agriculture and Food Security*, *3*(1), 3.

Xiao-Feng, H., Hai-Quan, C., Lin-Chuan, J., Lu, S., Xiao-Xiao, L., & Ye, C. (2021). Antitumor secondary metabolites of an endophytic fungus *Aspergillus terreus* TZS-201607 from *Pseudostellaria heterophylla*. *Natural Product Research and Development*, *33*(7), 1156.

Yaseen, R., Aziz, O., Saleem, M. H., Riaz, M., Zafar-ul-Hye, M., Rehman, M., … El-Serehy, H. A. (2020). Ameliorating the drought stress for wheat growth through application of ACC-deaminase containing rhizobacteria along with biogas slurry. *Sustainability*, *12*(15), 6022.

Yasmin, H., Bano, A., Wilson, N. L., Nosheen, A., Naz, R., Hassan, M. N., … Ahmad, P. (2022). Drought-tolerant *Pseudomonas* sp. showed differential expression of stress-responsive genes and induced drought tolerance in *Arabidopsis thaliana*. *Physiologia Plantarum*, *174*(1), e13497.

Yoo, S. -J., Shin, D. J., Won, H. Y., Song, J., & Sang, M. K. (2018). *Aspergillus terreus* JF27 promotes the growth of tomato plants and induces resistance against *Pseudomonas syringae* pv. *tomato*. *Mycobiology*, *46*(2), 147–153.

Zhang, Q., Gong, M., Yuan, J., Hou, Y., Zhang, H., Wang, Y., & Hou, X. (2017). Dark septate endophyte improves drought tolerance in Sorghum. *International Journal of Agriculture and Biology*, *19*(1), 53–60.

Zhou, R., Yu, X., Ottosen, C. -O., Rosenqvist, E., Zhao, L., Wang, Y., . . . Wu, Z. (2017). Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress. *BMC Plant Biology*, *17*(1), 1–13.

Zou, Y. -N., Wu, Q. -S., Huang, Y. -M., Ni, Q. -D., & He, X. -H. (2013). Mycorrhizal-mediated lower proline accumulation in *Poncirus trifoliata* under water deficit derives from the integration of inhibition of proline synthesis with increase of proline degradation. *PLoS One*, *8*(11), e80568.

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